Overview: Underground Plants

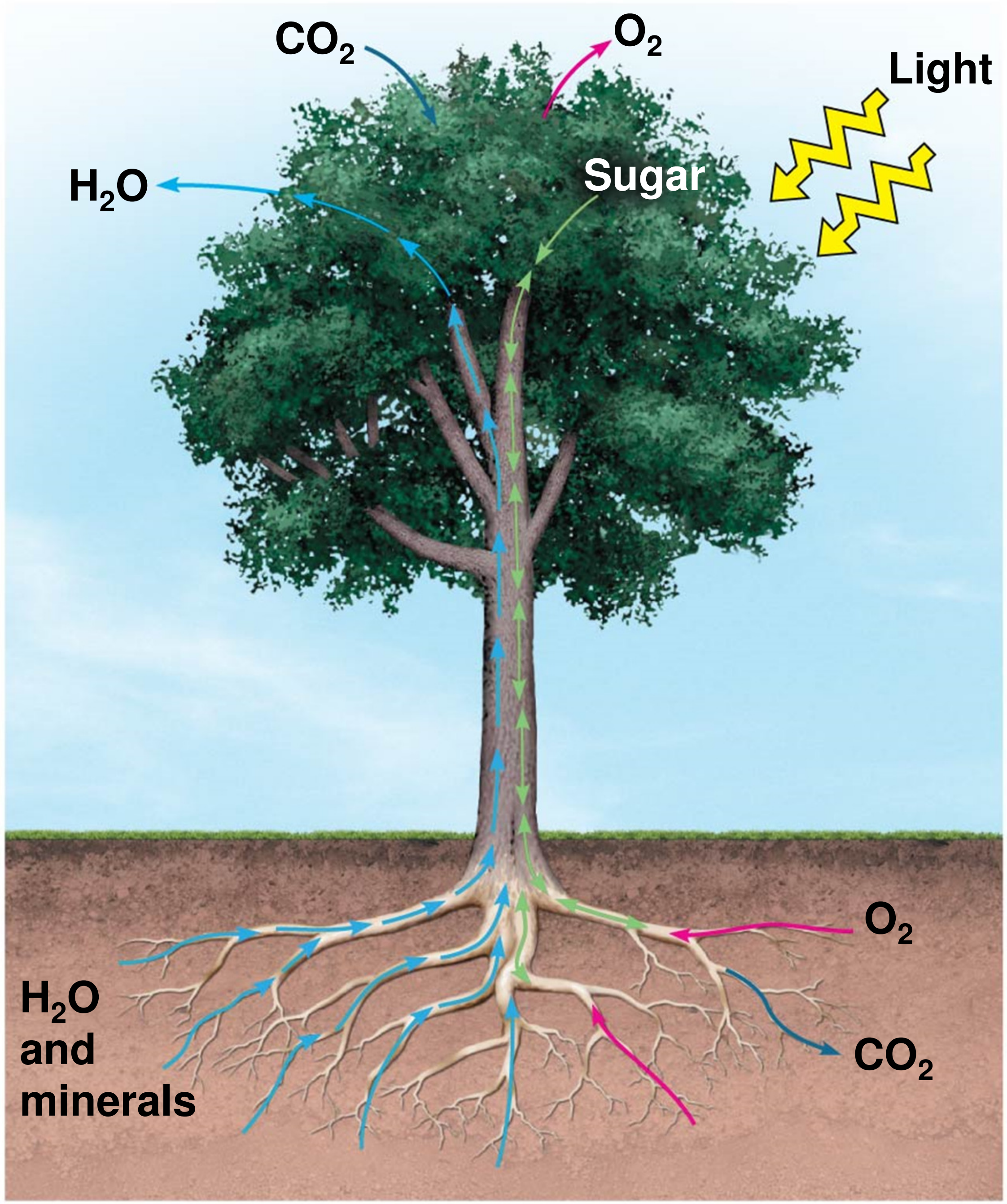
- The success of plants depends on their ability to gather and conserve resources from their environment
  - Often trade-offs in specialization
- The transport of materials is central to the integrated functioning of the whole plant

Concept 29.1: Adaptations for acquiring resources were key steps in the evolution of vascular plants

- The evolution of adaptations enabling plants to acquire resources from both above and below ground sources allowed for the successful colonization of land by vascular plants
  - The algal ancestors of land plants absorbed water, minerals, and CO_2 directly from surrounding water
  - Early nonvascular land plants lived in shallow water and had aerial shoots
- As land plants evolved, natural selection favored taller plants with flat appendages, multicellular branching roots, and efficient transport

- The evolution of xylem and phloem in land plants made possible the development of extensive root and shoot systems that carry out long-distance transport
  - **Xylem** transports water and minerals from roots to shoots
  - **Phloem** transports photosynthetic products (sugars) from sources to sinks
- Adaptations in each species represent compromises between enhancing photosynthesis and minimizing water loss

Figure 29.2-3

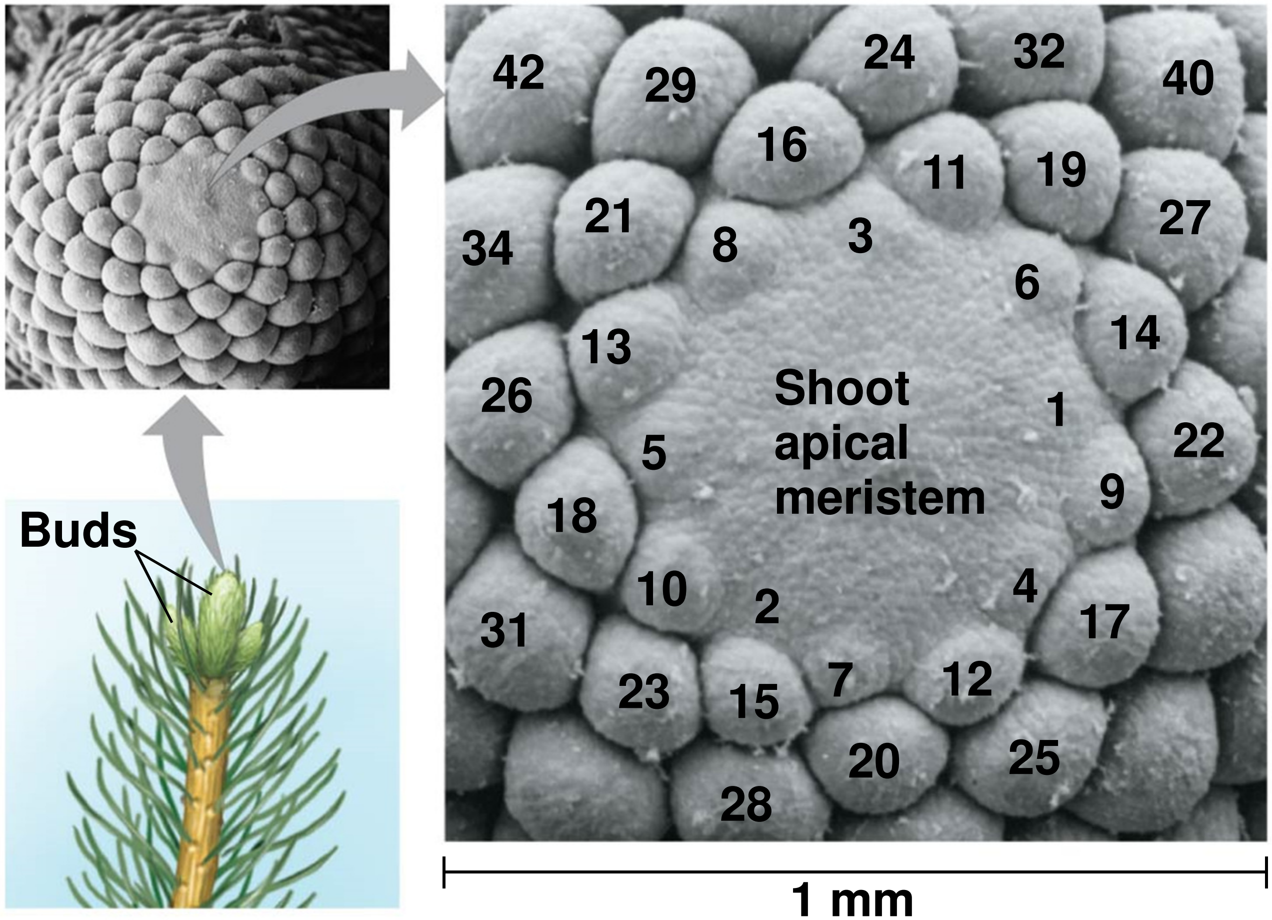


Shoot Architecture and Light Capture

- Stems serve as conduits for water and nutrients and as supporting structures for leaves
- Shoot height and branching pattern affect light capture
  - There is a trade-off between growing tall and branching

- **Phyllotaxy**, the arrangement of leaves on a stem, is specific to each species
  - Important in light capture!
  - Determined by shoot apical meristem
  - Most angiosperms have alternate phyllotaxy (one leaf per node) with leaves arranged in a spiral
    - The angle between leaves is 137.5° and likely minimizes shading of lower leaves

Figure 29.3


Buds
Shoot apical meristem
42
29
24
32
40
16
11
19
34
21
8
3
27
6
14
13
26
1
22
5
9
18
10
2
4
17
31
23
15
7
12
20
25
28
1 mm

- The productivity of each plant is affected by the depth of the **canopy**
  - The leafy portion of all the plants in the community
- Shedding of lower shaded leaves when they respire more than photosynthesize, *self-pruning*, occurs when the canopy is too thick

- Leaf orientation also affects light absorption
  - In low-light conditions, horizontal leaves capture more sunlight
  - In sunny conditions, vertical leaves are less damaged by sun and allow light to reach lower leaves

Root Architecture and Acquisition of Water and Minerals

- Soil is a resource mined by the root system
- Root growth can adjust to local conditions
  - For example, roots branch more in a pocket of high nitrate than in a pocket of low nitrate
- Roots are less competitive with other roots from the same plant than with roots from different plants

- Roots and the hyphae of soil fungi form mutualistic associations called mycorrhizae
    - Mutualisms with fungi helped plants colonize land
    - Mycorrhizal fungi increase the surface area for absorbing water and minerals

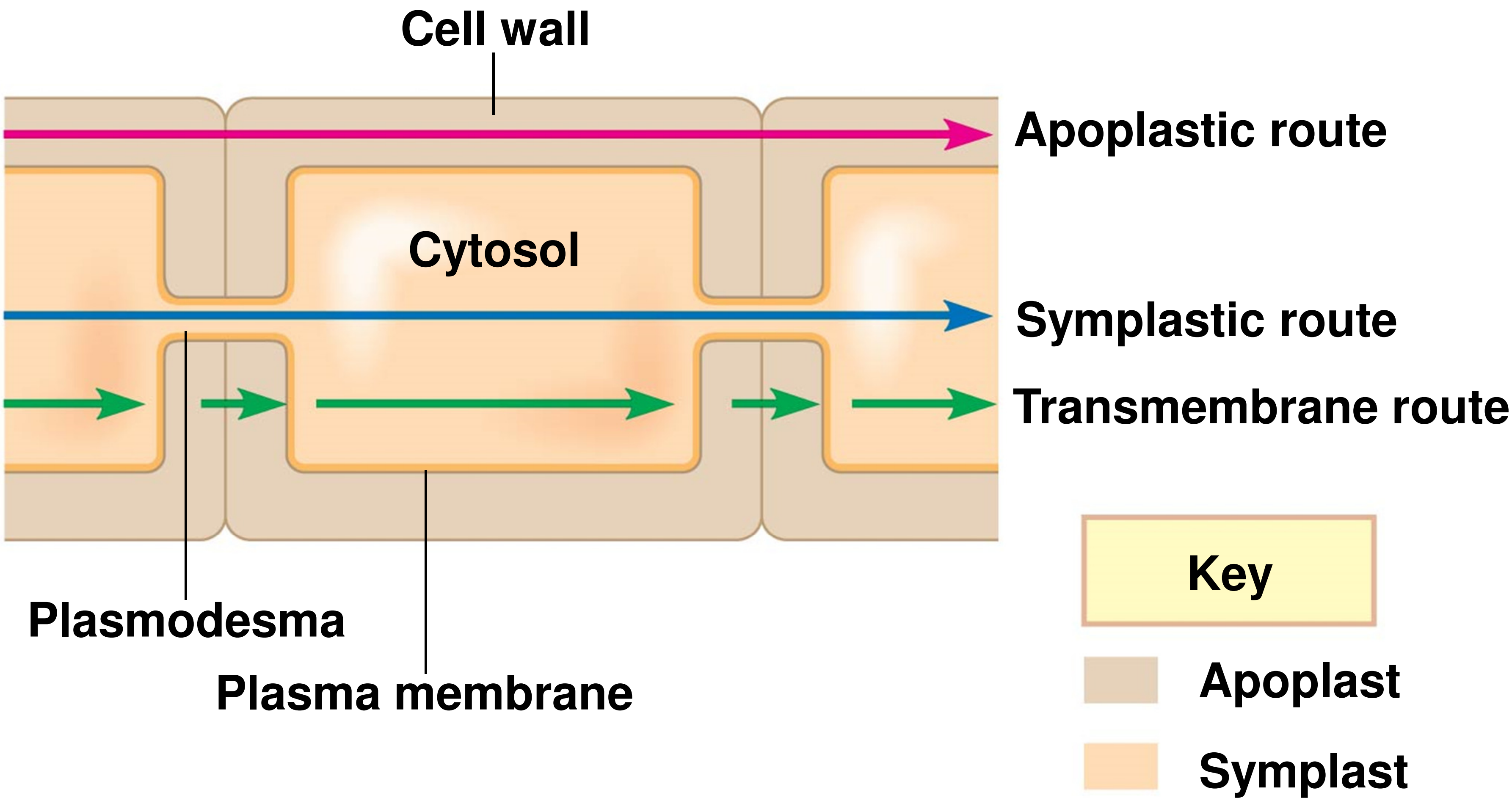
Concept 29.2: Different mechanisms transport substances over short or long distances

- There are two major transport pathways through plants
  - The **apoplast**
    - Consists of everything external to the plasma membrane
    - Includes cell walls, extracellular spaces, and the interior of vessel elements and tracheids
  - The **symplast**
    - Consists of the cytosol of the living cells in a plant, as well as the plasmodesmata

The Apoplast and Symplast: Transport Continuums

- Three transport routes for water and solutes are
  - The *apoplastic route*
    - Through cell walls and extracellular spaces
  - The *symplastic route*
    - Through the cytosol
    - Requires substances to cross a plasma membrane once but then can move via plasmodesmata
  - The *transmembrane route*
    - Across cell walls

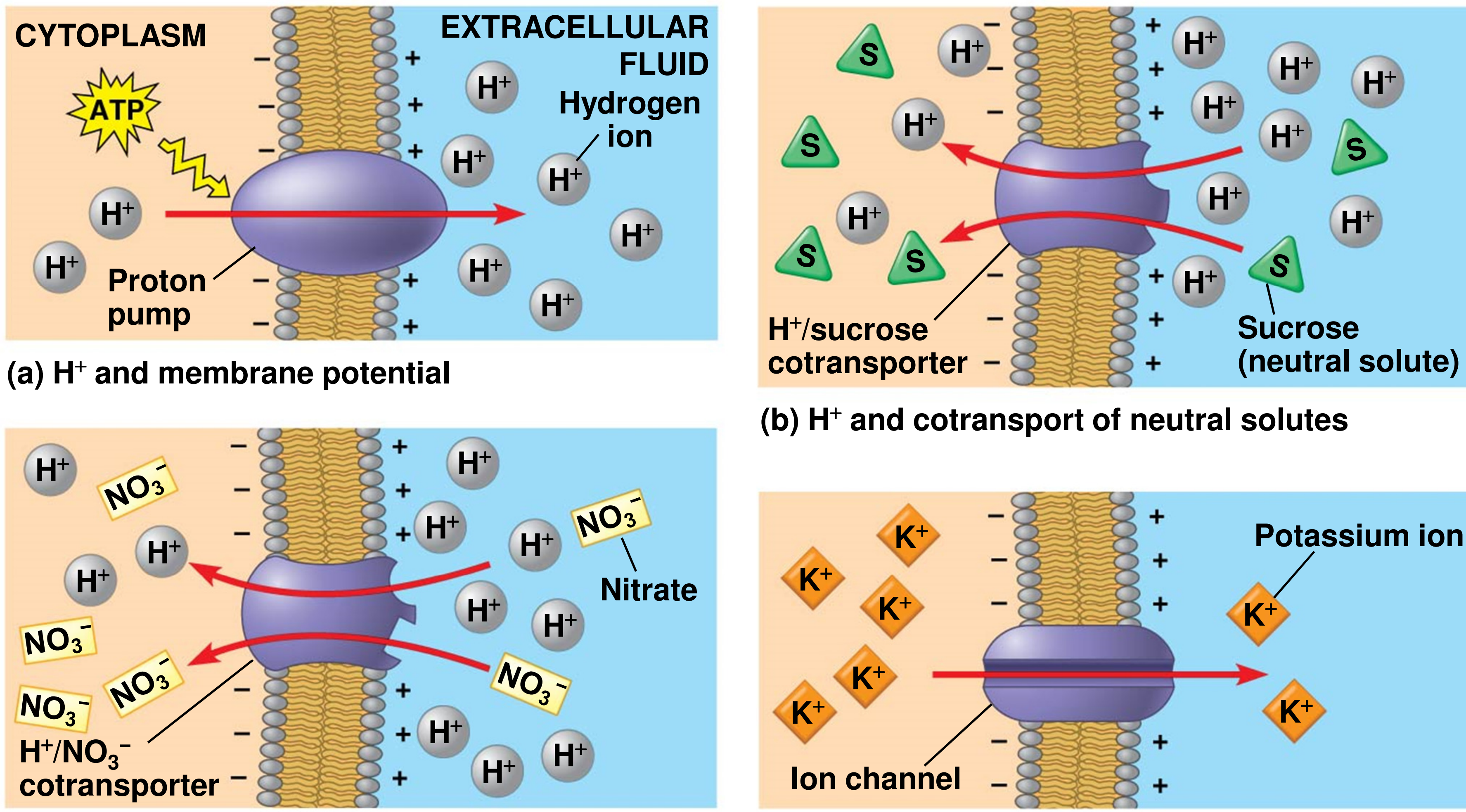
Figure 29.4


Cell wall
Apoplastic route
Cytosol
Symplastic route
Transmembrane route
Plasmodesma
Plasma membrane
Key
Apoplast
Symplast

Short-Distance Transport of Solutes Across Plasma Membranes

- Plasma membrane permeability controls short-distance movement of substances
- Both active and passive transport occur in plants
- In plants, membrane potential is established through pumping H^+ by proton pumps
  - Plant cells use the energy of H^+ gradients to cotransport other solutes by active transport
  - Plant cell membranes have ion channels that allow only certain ions to pass
- In animals, membrane potential is established through pumping Na^+ by sodium-potassium pumps

Figure 29.5



(a) H^+ and membrane potential

(b) H^+ and cotransport of neutral solutes

(c) H^+ and cotransport of ions

(d) Ion channels

Short-Distance Transport of Water Across Plasma Membranes

- To survive, plants must balance water uptake and loss
- **Osmosis** is the diffusion of free water across a membrane
  - Determines the net uptake or water loss by a cell
  - Is affected by solute concentration and pressure

- **Water potential** is a measurement that combines the effects of solute concentration and pressure
  - Determines the direction of movement of water
- Water flows from regions of higher water potential to regions of lower water potential
  - As a cell gains water, its water potential increases until equilibrium is reached
  - Potential refers to water's capacity to perform work
- Water potential is abbreviated as Ψ and measured in a unit of pressure called the **megapascal (MPa)**
- $\Psi = 0$ MPa for pure water at sea level and at room temperature

How Solutes and Pressure Affect Water Potential

- Both pressure and solute concentration affect water potential
- This is expressed by the water potential equation:

$$\Psi = \Psi_S + \Psi_P$$

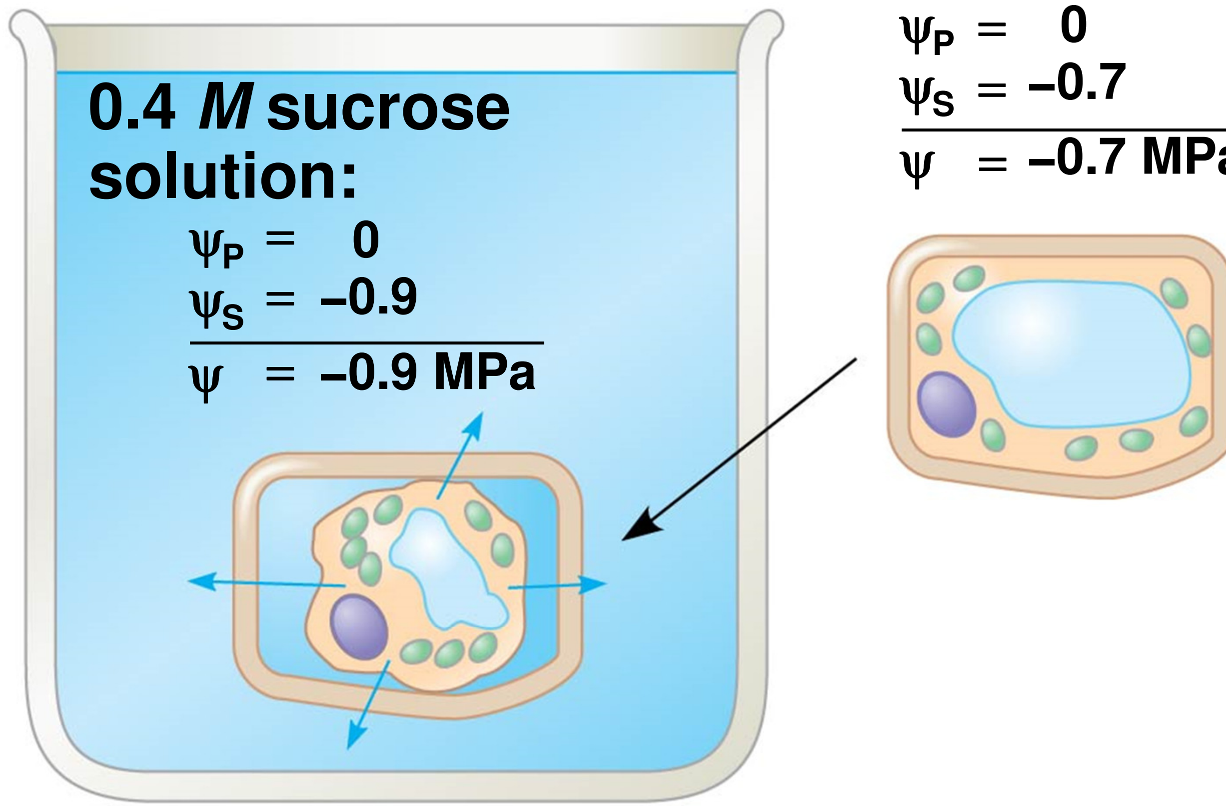
- The **solute potential (Ψ_S)** of a solution is directly proportional to its molarity
- Solute potential is also called osmotic potential
  - An increase in solutes has a negative effect on water potential
  - As solute concentration increases, Ψ_S becomes more negative

- **Pressure potential (Ψ_P)** is the physical pressure on a solution
  - Can be positive or negative relative to atmospheric pressure
- **Turgor pressure** is the internal pressure exerted by the plasma membrane against the cell wall, and the cell wall against the protoplast
  - The **protoplast** is the living part of the cell, which also includes the plasma membrane
- Turgor pressure helps maintain stiffness of plant tissues and is driving force for cell elongation
- Remember, water moves from regions of higher water potential to regions of lower water potential!

Water Movement Across Plant Cell Membranes

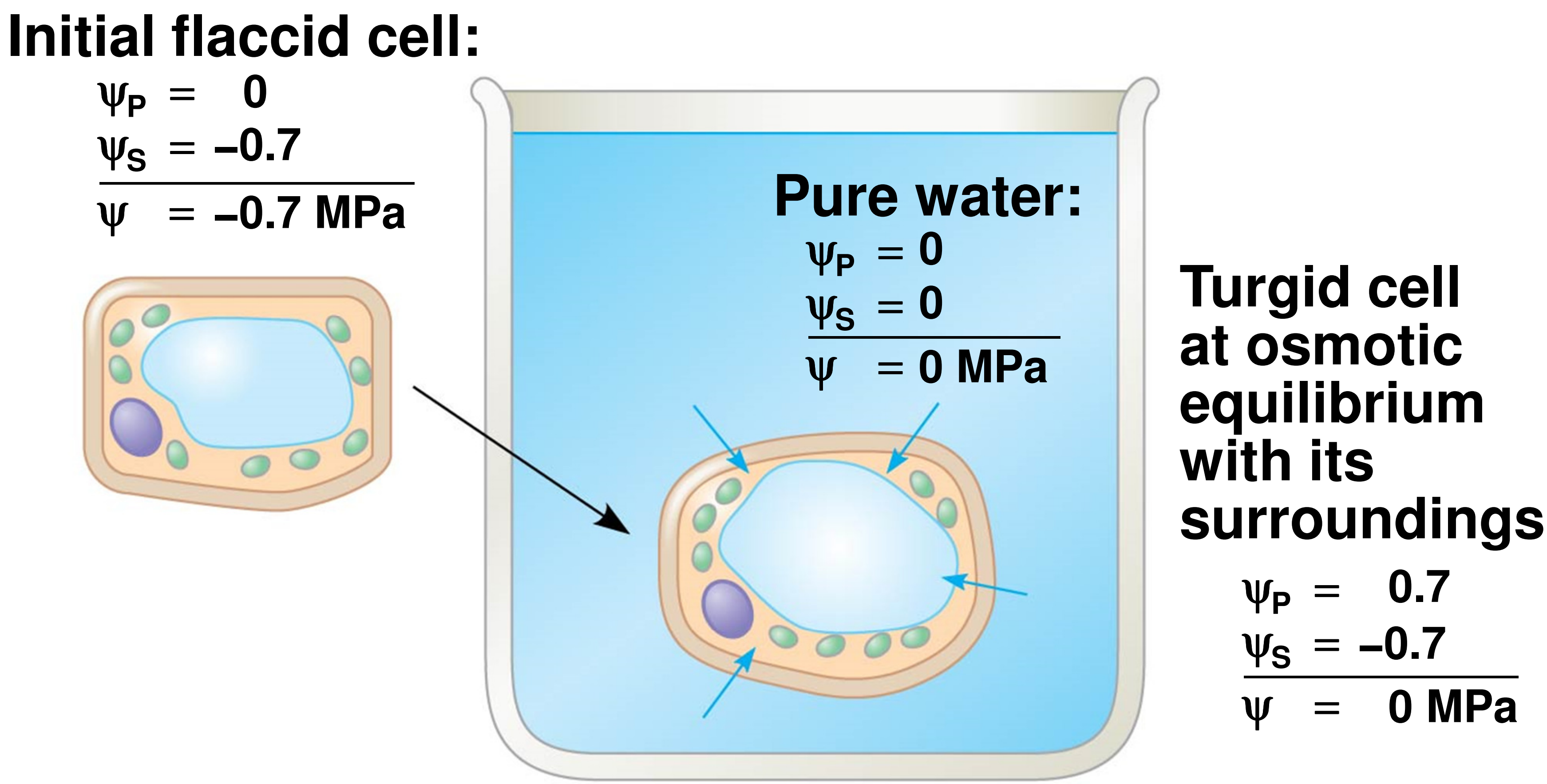
- Water potential affects uptake and loss of water by plant cells
- If a **flaccid** (limp) cell is placed in an environment with a higher solute concentration, the cell will lose water and undergo plasmolysis
  - **Plasmolysis** occurs when the protoplast shrinks and pulls away from the cell wall
- If a flaccid cell is placed in a solution with a lower solute concentration, the cell will gain water and become **turgid** (firm)
- Turgor loss in plants causes **wilting**, which can be reversed when the plant is watered

Figure 29.6a



(a) Initial conditions: cellular ψ > environmental ψ

Figure 29.6b



(b) Initial conditions:
cellular ψ < environmental ψ

Figure 29.7

Aquaporins: Facilitating Diffusion of Water

- Difference in water potential determines <u>direction</u> of water movement across membranes
- **Aquaporins** are transport proteins in the cell membrane that allow the passage of water
  - By opening and closing, these selective channels affect the <u>rate</u> of water movement across the membrane

Long-Distance Transport: The Role of Bulk Flow

- Efficient long-distance transport of fluid requires **bulk flow**
  - Movement of a fluid driven by pressure
  - Occurs from higher to lower pressure
  - Independent of solute concentration
- Water and solutes move together through tracheids and vessel elements of xylem and sieve-tube elements of phloem
- Efficient movement is possible because
  - Mature tracheids and vessel elements have no cytoplasm
  - Sieve-tube elements have few organelles in cytoplasm

Concept 29.3: Plants roots absorb essential elements from the soil

- Water, air, and soil minerals contribute to plant growth
  - Most of a plant's fresh mass is water
  - Most of a plant's dry mass consists of carbohydrates produced during photosynthesis
    - Thus carbon, oxygen, and hydrogen are the most abundant elements in dried plant residue

Macronutrients and Micronutrients

- Plants need 17 **essential elements**
  - Required for a plant to complete its life cycle
- Researchers use **hydroponic** culture to determine which chemical elements are essential
  - The growth of plants in mineral solutions
- 9 of the essential elements are called **macronutrients**
  - Plants require them in relatively large amounts
  - The macronutrients are carbon, oxygen, hydrogen, nitrogen, phosphorus, sulfur, potassium, calcium, and magnesium

Figure 29.8

Technique

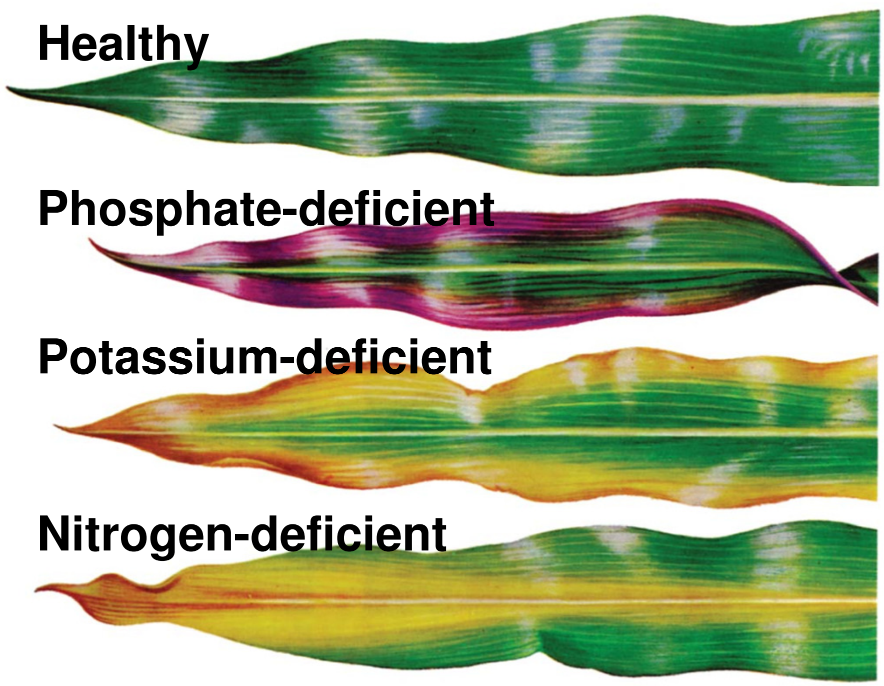
Control: Solution containing all minerals

Experimental: Solution without potassium

- The remaining eight essential elements are called **micronutrients**
  - Plants need them in very small amounts
  - The micronutrients are chlorine, iron, manganese, boron, zinc, copper, nickel, and molybdenum
- Plants with C_4 and CAM photosynthetic pathways also need sodium
- Too much of a nutrient can damage plants!
- Micronutrients function as cofactors
  - Nonprotein helpers in enzymatic reactions

Symptoms of Mineral Deficiency

- Symptoms of mineral deficiency depend on the nutrient's function and mobility within the plant
- The most common deficiencies are those of nitrogen, potassium, and phosphorus



Soil Management

- Ancient farmers recognized that crop yields would decrease on a particular plot over the years
- Soil management, by fertilization and other practices, allowed for agriculture and cities

Fertilization

- In natural ecosystems, nutrients are recycled through decomposition of feces and **humus**
  - Dead organic material
- Soils can become depleted of nutrients as plants and the nutrients they contain are harvested
- **Fertilization** replaces mineral nutrients that have been lost from the soil
- Excess minerals are often leached from the soil and can cause algal blooms in lakes

The Living, Complex Ecosystem of Soil

- Plants obtain most of their mineral nutrients from the topsoil
- Topsoil is formed when mineral particles released from weathered rock mix with living organisms and humus
- Inorganic, organic, and living components of soil are important to plants

Soil Texture

- Soil particles are classified by size
  - From largest to smallest they are called sand, silt, and clay
- Soil texture affects pore size
  - Larger particles = larger spaces between them
  - Important in terms of soil's ability to
    - Hold water and nutrients
    - Allow flow of water and air

- After a heavy rainfall, water drains from the larger spaces in the soil, but smaller spaces retain water because of its attraction to clay and other particles
- **Loams** are the most fertile topsoils and contain equal amounts of sand, silt, and clay
  - Small clay particles provide surface area for adhesion and retention of minerals and water
  - Large spaces between sand particles allows diffusion of oxygen to plant roots

Concept 29.4: Plant nutrition often involves relationships with other organisms

- Plants and soil microbes have a mutualistic relationship
  - Dead plants provide energy needed by soil-dwelling microorganisms
  - Secretions from living roots support a wide variety of microbes in the near-root environment

Soil Bacteria and Plant Nutrition

- Soil bacteria
  - Exchange chemicals with plant roots
  - Enhance decomposition
  - Increase nutrient availability

Rhizobacteria

- **Rhizobacteria** are soil bacteria that thrive in the **rhizosphere**
  - The soil layer surrounding the plant's roots and some can enter roots
- Rhizobacteria known as *plant-growth-promoting rhizobacteria* can play several roles
  - Produce hormones that stimulate plant growth
  - Produce antibiotics that protect roots from disease
  - Absorb toxic metals or make nutrients more available to roots

Bacteria in the Nitrogen Cycle

- Nitrogen can be an important limiting nutrient for plant growth
- The **nitrogen cycle** transforms atmospheric nitrogen and nitrogen-containing compounds
- Plants can only absorb nitrogen as either NO_3^- or NH_4^+
- Most usable soil nitrogen comes from actions of soil bacteria

Nitrogen-Fixing Bacteria: A Closer Look

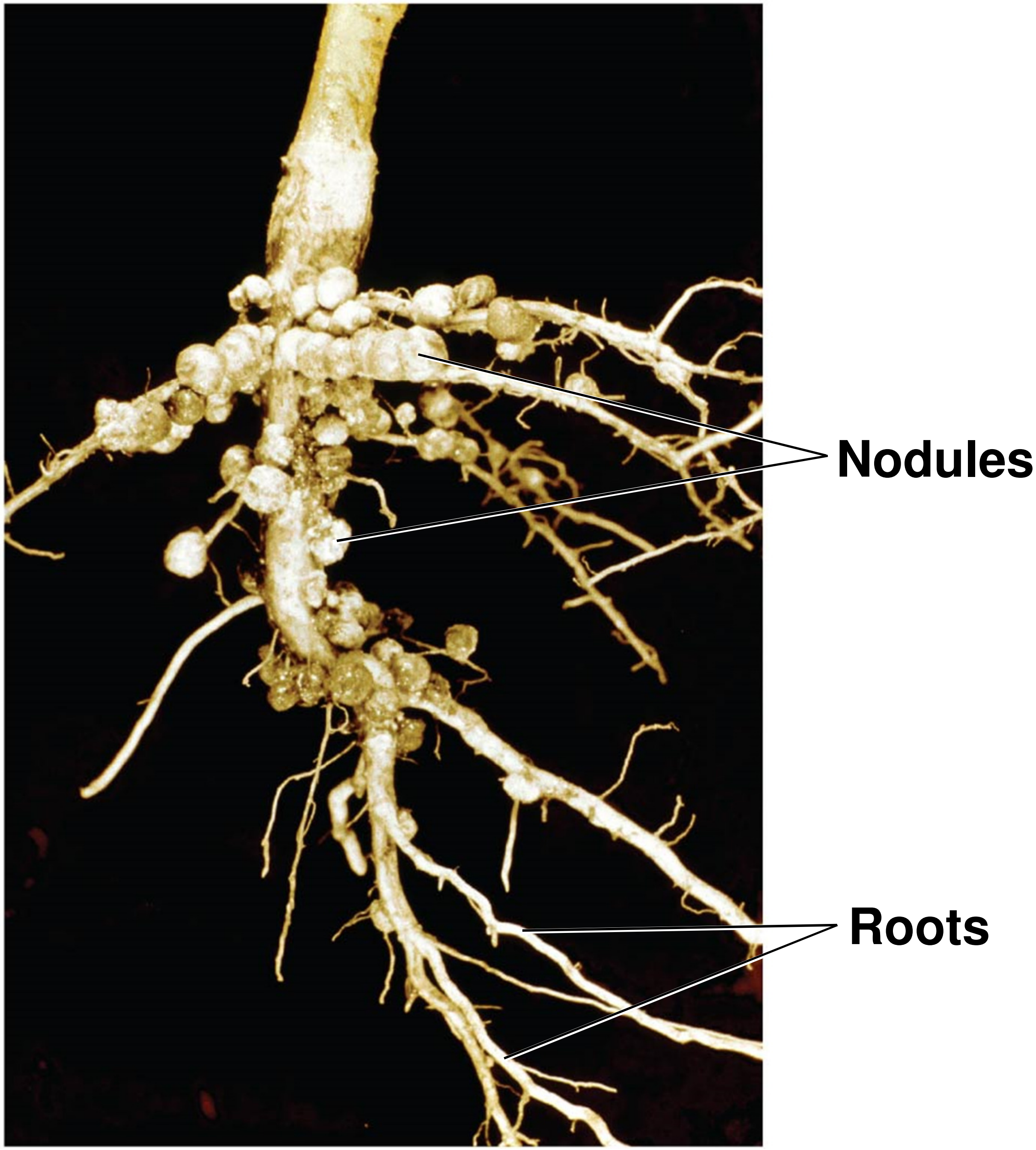
- Nitrogen is abundant in the atmosphere but unavailable to plants due to the triple bond between atoms in N_2
- **Nitrogen fixation** is the conversion of nitrogen from N_2 to NH_3
- Some nitrogen-fixing bacteria are free-living

Ⓟ$_i$

- Others form intimate associations with plant roots

- Symbiotic relationships with nitrogen-fixing *Rhizobium* bacteria provide some legumes with a source of fixed nitrogen
- Along a legume's roots are swellings called **nodules**, composed of plant cells "infected" by nitrogen-fixing *Rhizobium* bacteria
- An example of mutualism (both species benefit)
  - The plant obtains fixed nitrogen from *Rhizobium*
  - *Rhizobium* obtains sugar and an anaerobic environment

Figure 29.12



Fungi and Plant Nutrition

- **Mycorrhizae** are mutualistic associations of fungi and roots
  - The fungus benefits from a steady supply of sugar from the host plant
  - The host plant benefits because the fungus increases the surface area for water uptake and mineral absorption
- Mycorrhizal fungi also secrete
  - Growth factors that stimulate root growth and branching
  - Antibiotics

Epiphytes, Parasitic Plants, and Carnivorous Plants

- Some plants have nutritional adaptations that use other organisms in nonmutualistic ways
- Three unusual adaptations are
  - **Epiphytes** grow on other plants and obtain water and minerals from rain, rather than tapping their hosts for sustenance
  - **Parasitic plants** absorb water, sugars, and minerals from their living host plant
  - **Carnivorous plants** are photosynthetic but obtain nitrogen by killing and digesting mostly insects

Figure 29.15a

Staghorn fern, an epiphyte

Figure 29.15b

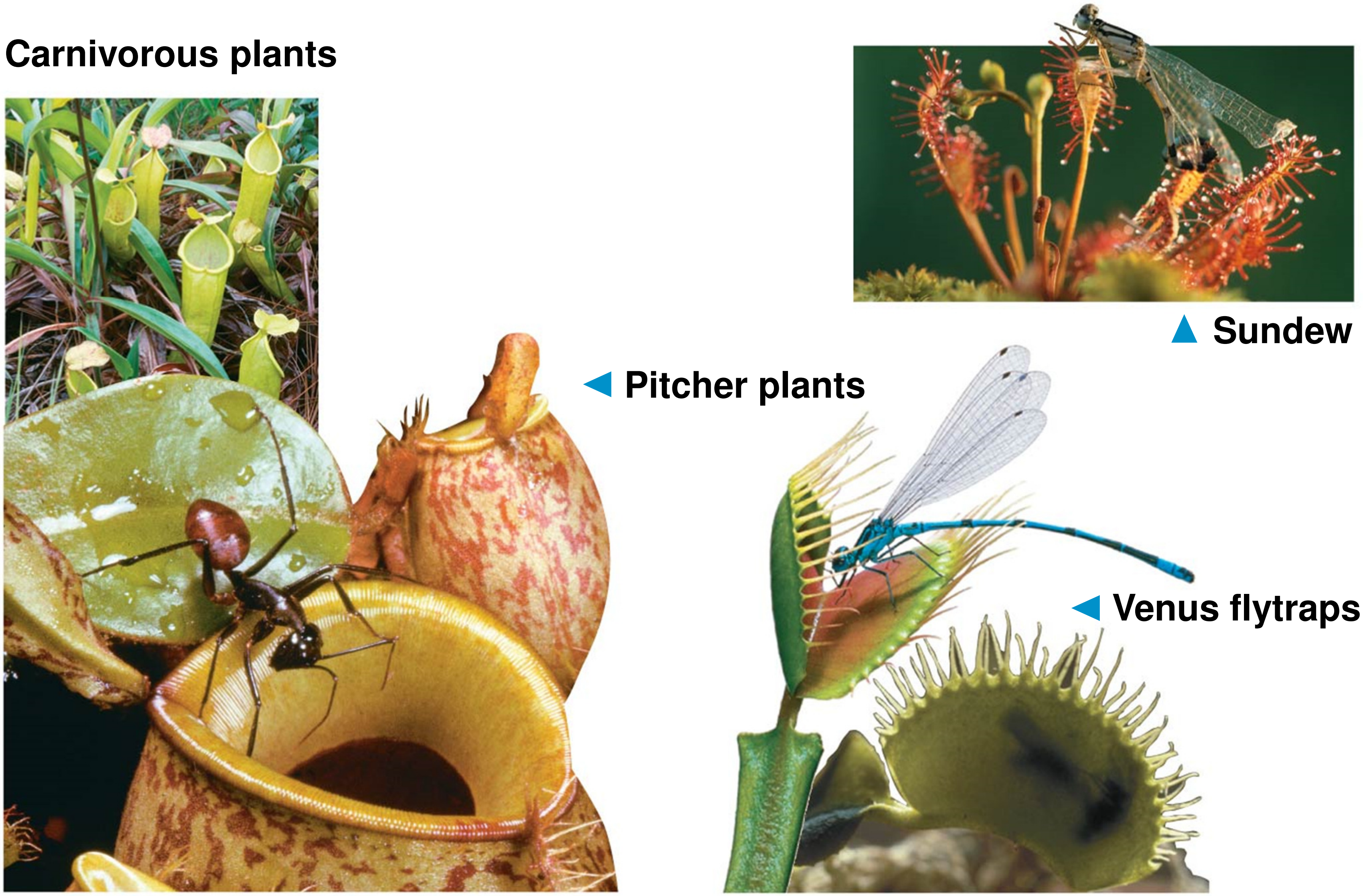
Parasitic plants

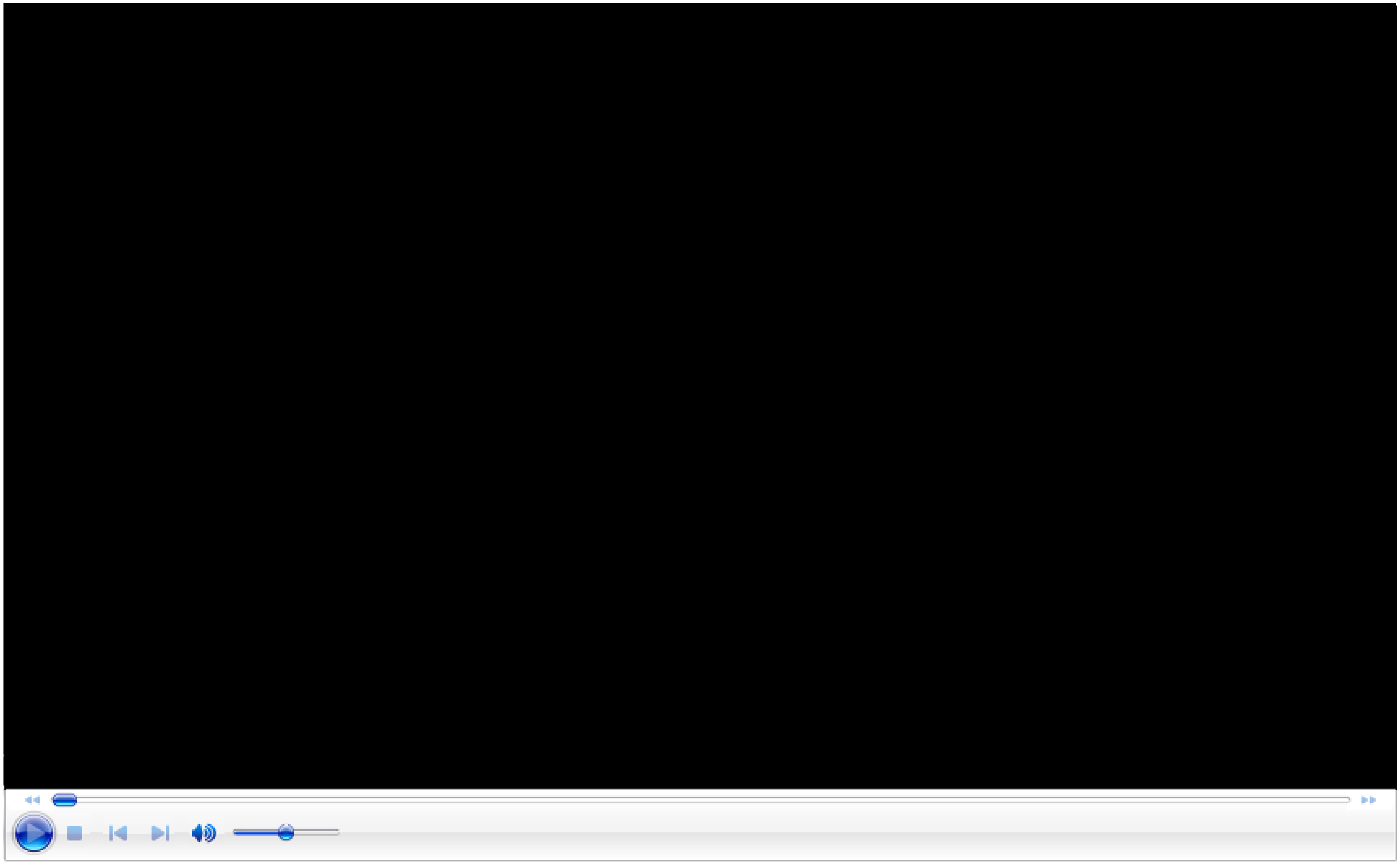
Mistletoe, a photosynthetic parasite

Dodder, a nonphoto-synthetic parasite (orange)

Indian pipe, a nonphoto-synthetic parasite of mycorrhizae

Figure 29.15c





Video: Sundew Traps Prey

Concept 29.5: Transpiration drives the transport of water and minerals from roots to shoots via the xylem

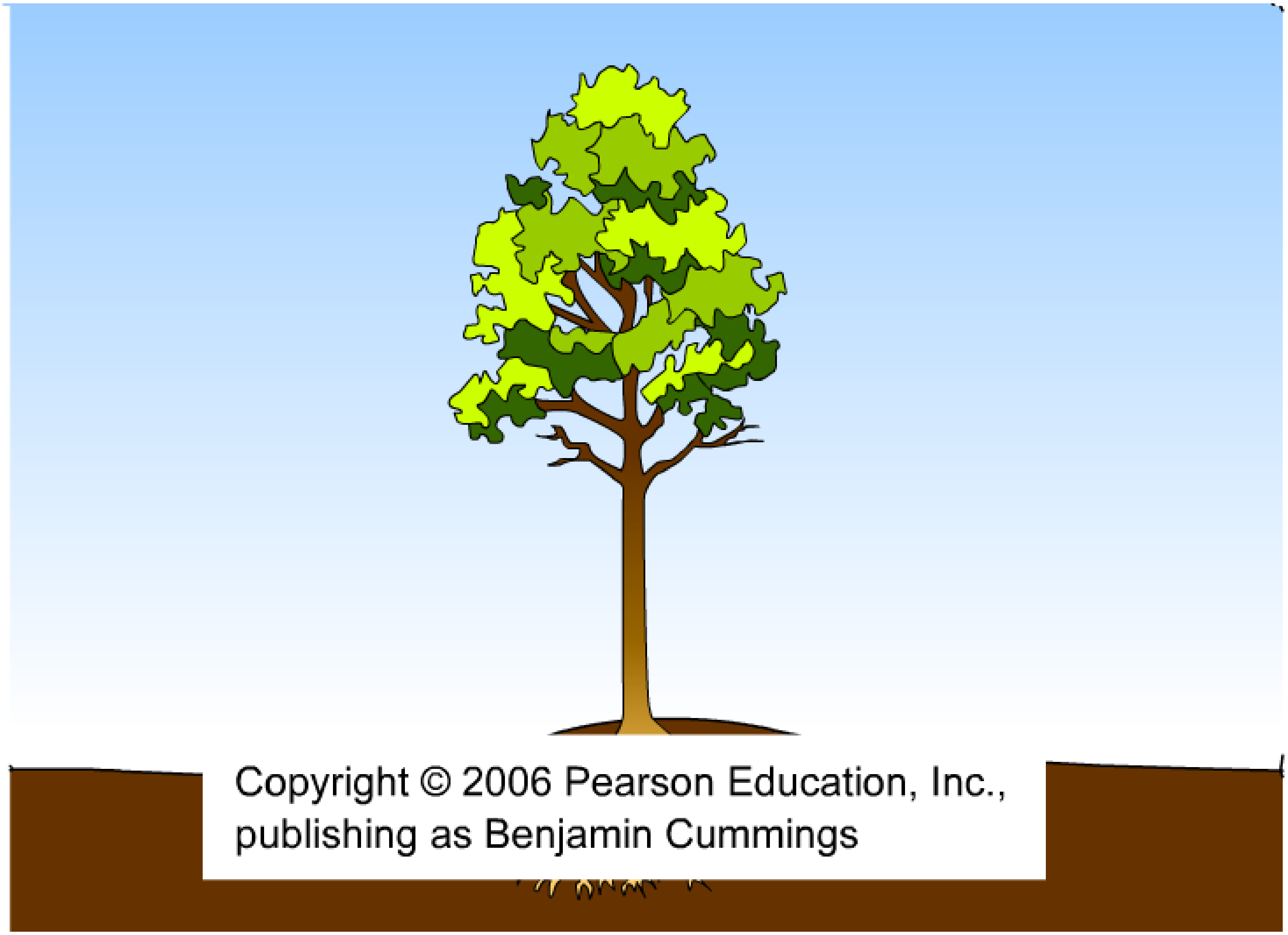
- Plants can move a large volume of water from their roots to shoots

Absorption of Water and Minerals by Root Cells

- Most water and mineral absorption occurs near root tips
  - Epidermis is permeable to water
  - Root hairs account for much of the absorption of water by roots
- After soil solution enters the roots, the extensive surface area of cortical cell membranes enhances uptake of water and selected minerals
- The concentration of essential minerals is greater in the roots than in the soil because of active transport

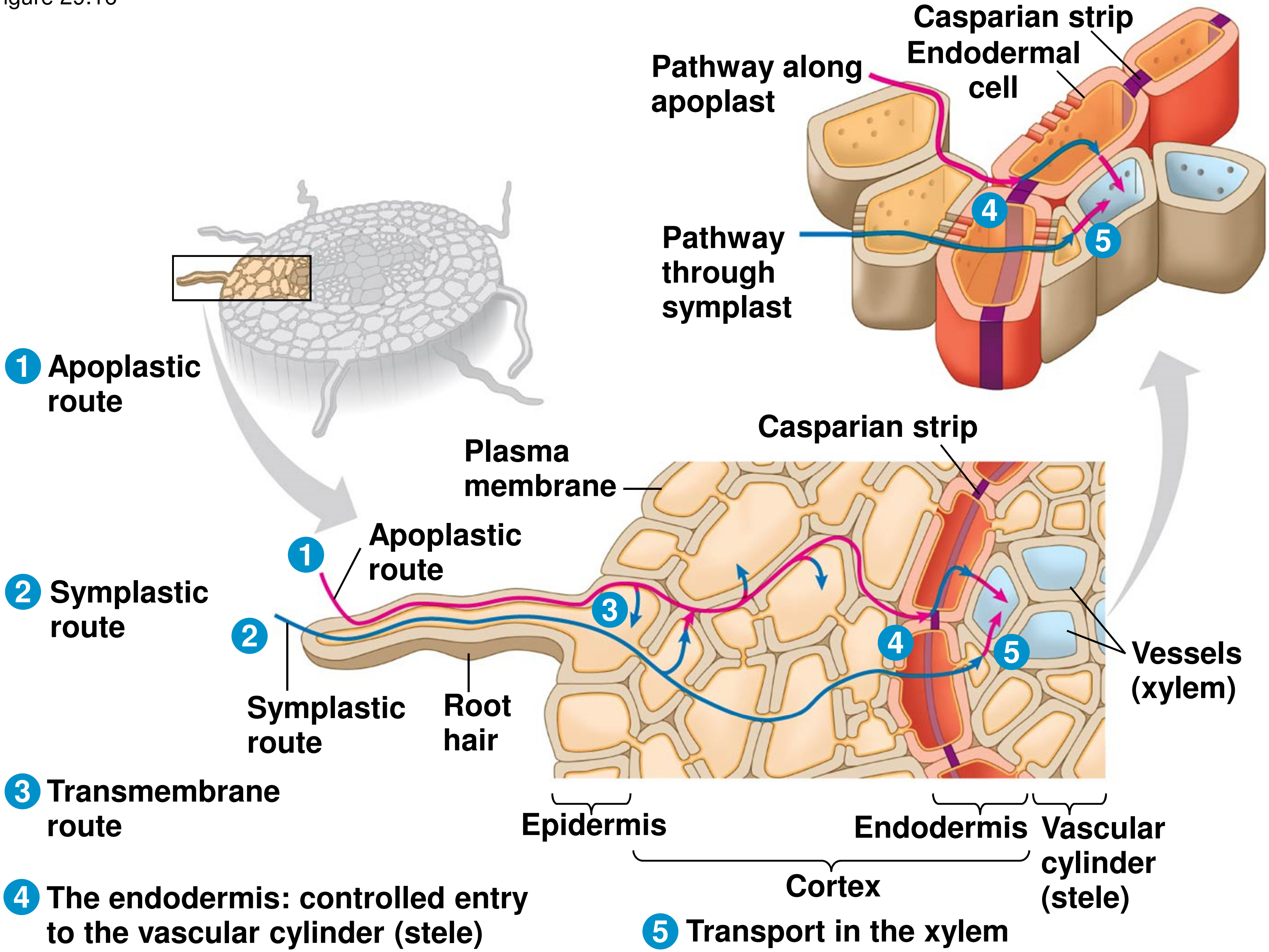
Transport of Water and Minerals into the Xylem

- In order to be transported to the rest of the plant, water and minerals must enter the xylem of the vascular cylinder, or stele
- The **endodermis** is the innermost layer of cells in the root cortex and surrounds the vascular cylinder
  - The last checkpoint for selective passage of minerals from the cortex into the vascular tissue
- Water can cross the cortex via the symplast or apoplast



Animation: Transport in Roots
Right click slide / Select play

Figure 29.16



1 Apoplastic route
2 Symplastic route
3 Transmembrane route
4 The endodermis: controlled entry to the vascular cylinder (stele)
5 Transport in the xylem
Casparian strip
Endodermal cell
Pathway along apoplast
Pathway through symplast
4
5
Plasma membrane
Casparian strip
1
Apoplastic route
2
3
4
5
Symplastic route
Root hair
Vessels (xylem)
Epidermis
Endodermis
Vascular cylinder (stele)
Cortex

- Water and minerals can travel to the vascular cylinder through the cortex via
  - The apoplastic route, along cell walls and extracellular spaces
  - The symplastic route, in the cytoplasm, moving between cells through plasmodesmata
  - The transmembrane route, moving from cell to cell by crossing cell membranes and cell walls

- The waxy **Casparian strip** of the endodermal wall blocks apoplastic transfer of minerals from the cortex to the vascular cylinder
  - Forces water and minerals in the apoplast to cross the plasma membrane of an endodermal cell to enter the vascular cylinder
  - Ensures that no minerals can reach the vascular tissue of the root without crossing a selectively permeable membrane
  - Also prevents solutes in xylem from leaking back out

- The endodermis regulates and transports needed minerals from the soil into the xylem
- Water and minerals move from the protoplasts of endodermal cells into their cell walls
- Diffusion and active transport are involved in this movement from symplast to apoplast
- Water and minerals now enter the tracheids and vessel elements
  - Transported to shoot system by bulk flow

Bulk Flow Transport via the Xylem

- Water and minerals from soil enter plant through epidermis, cross root cortex, and pass into vascular cylinder
- **Xylem sap**, water and dissolved minerals, is transported from roots to leaves by bulk flow
  - Much faster than diffusion or active transport
- The transport of xylem sap involves **transpiration**
  - The loss of water vapor from a plant's surface
- Transpired water is replaced as water travels up from the roots

Pulling Xylem Sap: The Cohesion-Tension Hypothesis

- According to the **cohesion-tension hypothesis**, transpiration and water cohesion pull water from shoots to roots
  - Xylem sap is normally under negative pressure, or tension

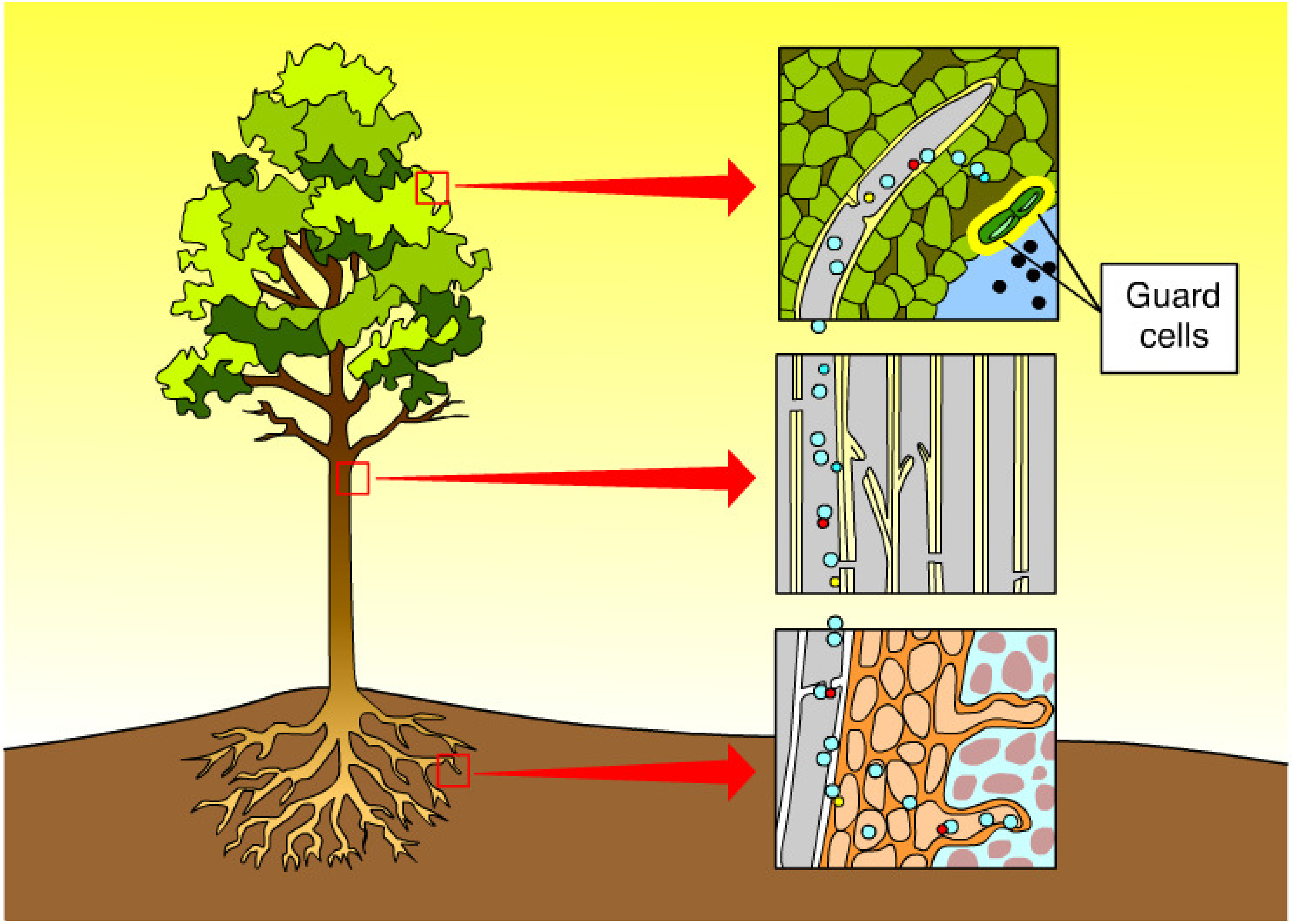
Transpirational Pull

- Typically, the air outside the leaf is drier
  - Has lower water potential than air inside the leaf
  - So water vapor diffuses down its water potential gradient and exits the leaf via stomata
    - Loss of water vapor by diffusion and evaporation is called transpiration
- Negative pressure potential develops at the surface of mesophyll cell walls in the leaf
- This causes water to move up through the xylem
  - The pulling effect results from the cohesive binding between water molecules

- Negative pressure potential lowers water potential
  - Water moves form areas of higher water potential to lower water potential
- The transpirational pull on xylem sap is transmitted from leaves to roots
- Transpirational pull depends on water’s adhesion, cohesion, and surface tension

Cohesion and adhesion in the ascent of xylem sap

- Water molecules are attracted to each other through cohesion
  - Cohesion makes it possible to pull a column of xylem sap
- Water molecules are attracted to hydrophilic walls of xylem cell walls through adhesion
  - Adhesion of water molecules to xylem cell walls helps offset the force of gravity
- The tension produced by transpirational pull lowers water potential in root xylem
  - Causes water to flow passively from soil, across root cortex, into vascular cylinder



Animation: Transpiration
Right click slide / Select play

Figure 29.18

Outside air ψ
= □100.0 MPa

Leaf ψ (air spaces)
= □7.0 MPa

Leaf ψ (cell walls)
= □1.0 MPa

Trunk xylem ψ
= –0.8 MPa

Trunk xylem ψ
= –0.6 MPa

Soil ψ
= –0.3 MPa

Water potential gradient

Xylem sap
Mesophyll cells
Stoma
Water molecule
Atmosphere
Transpiration

Adhesion by hydrogen bonding
Xylem cells
Cell wall
Cohesion by hydrogen bonding
Cohesion and adhesion in the xylem

Water molecule
Root hair
Soil particle
Water
Water uptake from soil

- Thick secondary walls prevent vessel elements and tracheids from collapsing under negative pressure
- Drought stress or freezing can cause cavitation
  - The formation of a water vapor pocket by a break in the chain of water molecules

Xylem Sap Ascent by Bulk Flow: *A Review*

- Bulk flow is driven by a water potential difference at opposite ends of xylem tissue
- Bulk flow is driven by evaporation
  - Does NOT require energy from the plant
  - Like photosynthesis, it is solar powered

- Bulk flow differs from diffusion
  - It is driven by differences in pressure potential, not solute potential
  - It occurs in hollow dead cells, not across the membranes of living cells
  - It moves the entire solution, not just water or solutes
  - It is much faster

Concept 29.6: The rate of transpiration is regulated by stomata

- Leaves generally have broad surface areas and high surface-to-volume ratios
- These characteristics increase photosynthesis and increase water loss through stomata
- Guard cells help balance water conservation with gas exchange for photosynthesis

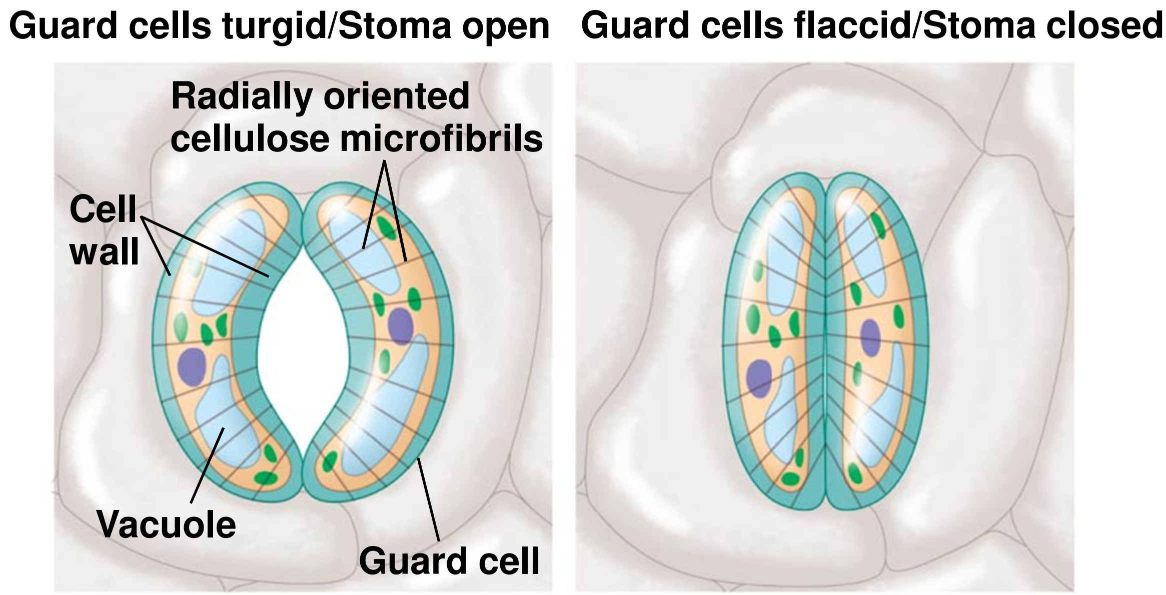
Stomata: Major Pathways for Water Loss

- Waxy cuticle limits water loss in most of leaf
  - Most of the water lots escapes through stomata
- Each stoma is flanked by a pair of guard cells
  - Control the diameter of the stoma by changing shape

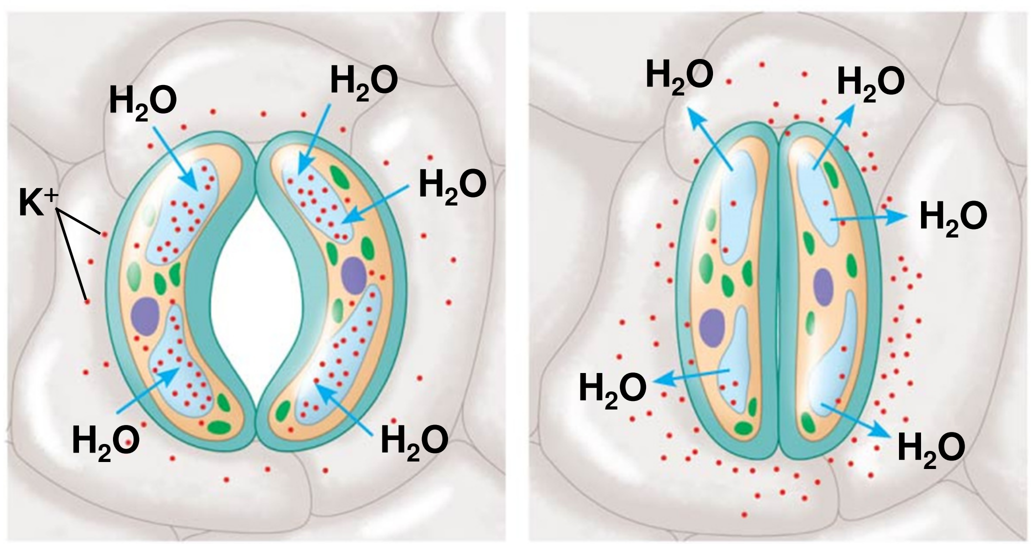
Mechanisms of Stomatal Opening and Closing

- Changes in turgor pressure open and close stomata
  - When turgid, guard cells bow outward and the pore between them opens
  - When flaccid, guard cells become less bowed and the pore closes
- Changes in turgor pressure result primarily from the reversible uptake and loss of potassium ions (K^+) by the guard cells
  - Stomata open when guard cells actively accumulate K^+ form neighboring epidermal cells
  - Stomata close when guard cells lose K^+, which leads to an osmotic loss of water

Figure 29.19



(a) Changes in guard cell shape and stomatal opening and closing (surface view)



(b) Role of potassium ions (K^+) in stomatal opening and closing

Stimuli for Stomatal Opening and Closing

- Generally, stomata open during the day and close at night to minimize water loss
- Stomatal opening at dawn is triggered by
  - Light
  - CO_2 depletion
  - An internal "clock" in guard cells
- All eukaryotic organisms have internal clocks
  - **Circadian rhythms** are 24-hour cycles

- Drought stress can cause stomata to close during the daytime
- The hormone **abscisic acid (ABA)** is produced in response to water deficiency and causes the closure of stomata
  - Reduces wilting
  - Also restricts CO_2 absorption, slowing photosynthesis

Effects of Transpiration on Wilting and Leaf Temperature

- Plants lose a large amount of water by transpiration
  - Evaporation is increased on sunny, warm, dry, and windy days
- If the lost water is not replaced by sufficient transport of water, the plant will lose water and wilt
- Transpiration also results in evaporative cooling
  - Can lower the temperature of a leaf and prevent protein denaturation

Adaptations That Reduce Evaporative Water Loss

- **Xerophytes** are plants adapted to arid climates
- Some desert plants complete their life cycle during the rainy season
- Others have leaf modifications that reduce the rate of transpiration
- Some plants use a specialized form of photosynthesis called **crassulacean acid metabolism (CAM)**
  - Stomata remain closed during the day, so gas exchange occurs at night

Figure 29.20

► **Ocotillo (*Fouquieria splendens*)**

▼ **Oleander (*Nerium oleander*)**

Thick cuticle

Upper epidermal tissue

Trichomes (“hairs”)

Crypt

Stoma

Lower epidermal tissue

100 µm

► **Old man cactus (*Cephalocereus senilis*)**

Concept 29.7: Sugars are transported from sources to sinks via the phloem

- Water and minerals flow upward from soil to roots to leaves through xylem
- The products of photosynthesis (sugars) are transported through phloem by the process of **translocation**
  - Generally opposite direction, from leaves to roots

Movement from Sugar Sources to Sugar Sinks

- In angiosperms, sieve-tube elements are the conduits for translocation
- **Phloem sap** is an aqueous solution that is high in sucrose
- It travels from a sugar source to a sugar sink
  - A **sugar source** is an organ that is a net producer of sugar, such as mature leaves
  - A **sugar sink** is an organ that is a net consumer or storer of sugar, such as a tuber or bulb
    - A storage organ can be both a sugar sink in summer and sugar source in winter

- Sugar must be loaded into sieve-tube elements before being exported to sinks
- Depending on the species, sugar may move by symplastic or both symplastic and apoplastic pathways
- Companion cells enhance solute movement between the apoplast and symplast

- In most plants, phloem loading requires active transport
  - Proton pumping and cotransport of sucrose and H^+ enable the cells to accumulate sucrose
- At the sink, sugar molecules diffuse from the phloem to sink tissues and are followed by water

Figure 29.21a

Mesophyll cell

Cell walls (apoplast)

Plasma membrane

Plasmodesmata

Companion (transfer) cell

Sieve-tube element

Mesophyll cell

Bundle-sheath cell

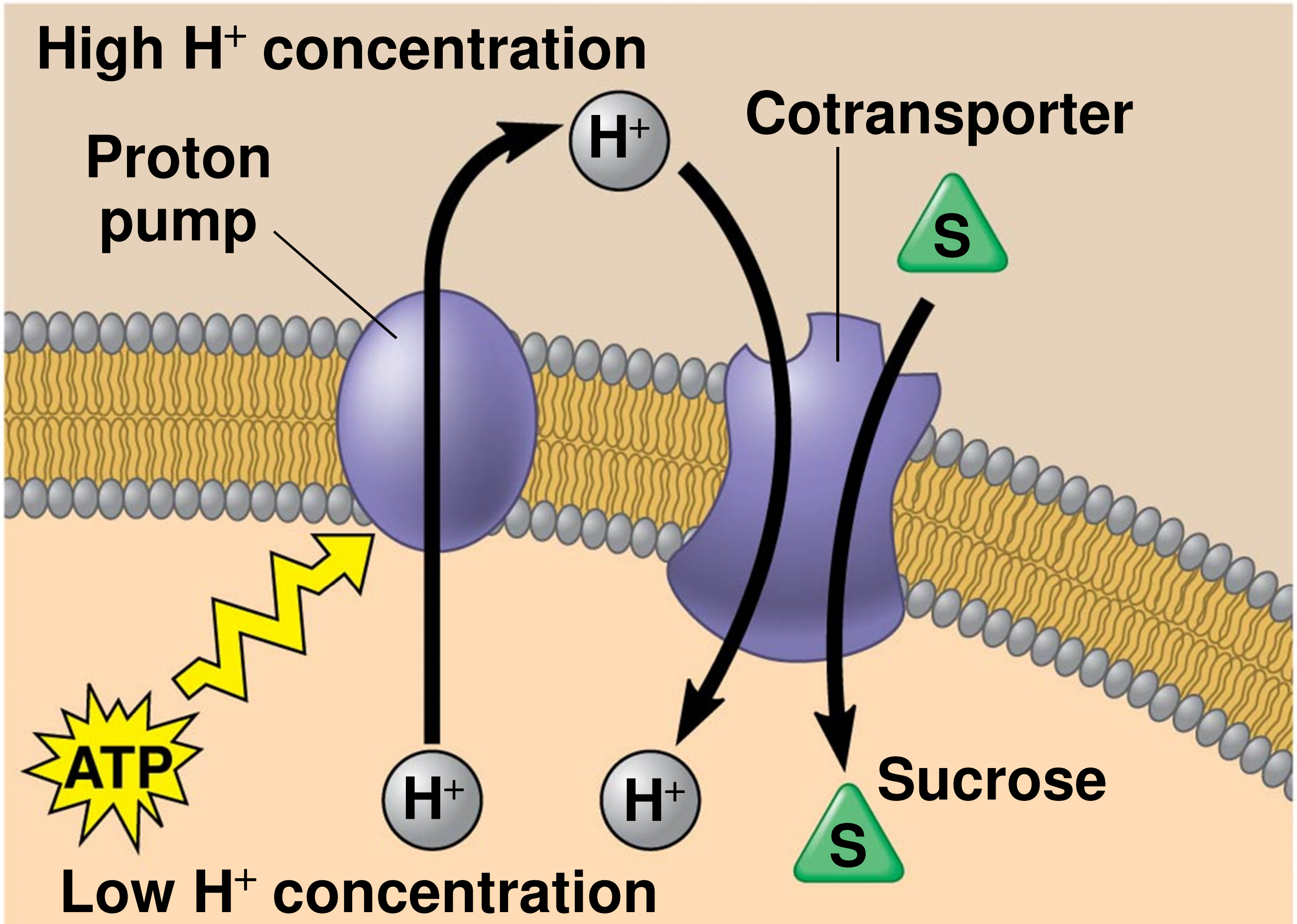
Phloem parenchyma cell

Apoplast

Symplast

(a) Sucrose manufactured in mesophyll cells can travel via the symplast (blue arrows) to sieve-tube elements.

Figure 29.21b

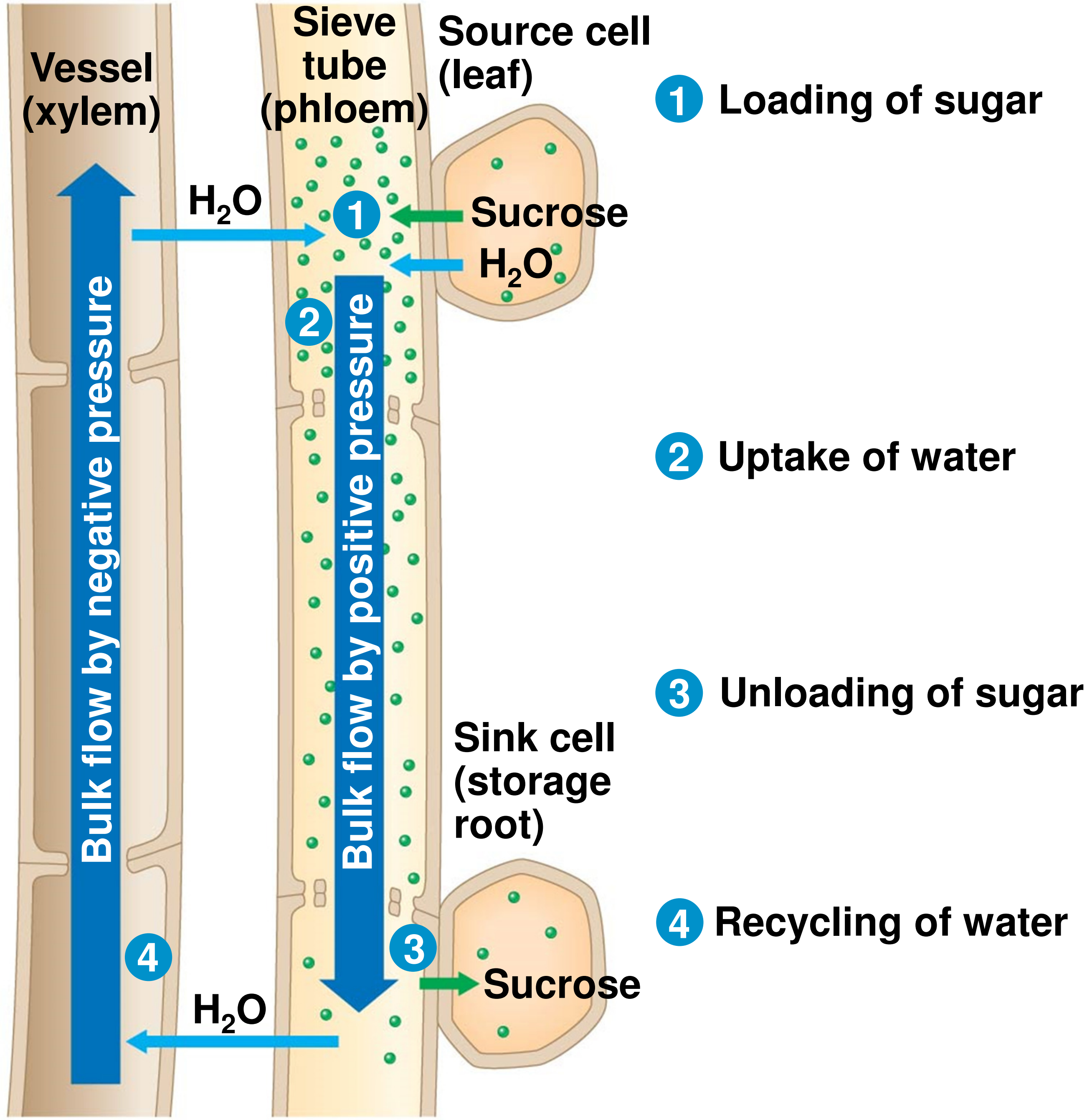


(b) A chemiosmotic mechanism is responsible for the active transport of sucrose.

Bulk Flow by Positive Pressure: The Mechanism of Translocation in Angiosperms

- Phloem sap moves through a sieve tube by bulk flow driven by positive pressure called *pressure flow*
- Sometimes there are more sinks than can be supported by sources
  - *Self-thinning* is the dropping of sugar sinks such as flowers, seeds, or fruits

Figure 29.22



Vessel (xylem)
Sieve tube (phloem)
Source cell (leaf)
H2O
1
Sucrose
H2O
2
Bulk flow by negative pressure
Bulk flow by positive pressure
Sink cell (storage root)
3
Sucrose
4
H2O
1 Loading of sugar
2 Uptake of water
3 Unloading of sugar
4 Recycling of water

Figure 29.UN03